DEVELOPMENT AND THE FORMATION OF COLONIES IN POCILLOPORA AND PORITES.—PART I

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WITH SIXTEEN TEXT-FIGURES AND SIX PLATES

BRITISH MUSEUM NATURAL HISTORY

CONTENTS

I. INTRODUCTION.

IN his recent account (1929) of the post-larval development of *Maeandra* (*Manicina*) *areolata,* Boschma summarizes the data which exist on the development of the Madreporaria ; they are strikingly few, and mainly concern the earlier phases. Edmondson, working at the Marine Biological Laboratory of the University of Hawaii, at Waikiki, has recently reared larvae of *Dendrophyllia manni*, *Pocillopora cespitosa*, and *Cyphastrea ocellina*. He has published a short account (1929) of the development of these species, but does not go into detail. Such data as are given with regard to *Pocillopora cespitosa* suggest that many of the details of development in that species are different from those of *P. bulbosa,* as described below.

Matthai, in his notable paper of 1926 on colony-formation in Astraeid corals, remarks (p. 313) that " Colony-formation in the Madreporaria was generally described as taking place by two principal methods, viz. budding and fission. This statement was based on the study of the hard parts, which were examined without reference to the polyps that formed them"; and later, "it is now clear that no reliable data on colony-formation can be obtained from a study of coralla only," and "stages in the budding of the polyps of Astraeid colonies are herein described for the first time." Even with the data obtained by Matthai, added to those available from earlier work (especially from the classical papers of Duerden), we are still limited almost entirely, for our knowledge of budding in the Madreporaria, to information procured by examination of young colonies and of the growing regions of older ones, whether externally on living material, or by means of sectioning fixed and decalcified colonies. So far as I am aware, apart from the data given by Edmondson, this paper describes for the first time the budding of reef-corals actually witnessed on the living colony, from the extrusion of the planula onward, over a considerable period of time. This is a little remarkable, in the year 1930, when we consider that even the older text-books speak of asexual reproduction in the Madreporaria as if a considerable body of knowledge relating to it were extant; but it is in fact natural enough, because the long residence on a coral reef which is the first condition of its attainment, together with the facilities for rearing larvae, are not everyday occurrences.

In the present paper only the outlines of the story are told; in Part II the anatomical details, together with a discussion, will be provided.

I am very much indebted to F. Pittock (Department of Embryology, University College, London) for the beautiful photomicrographs here reproduced; to Eleanor Dale for two drawings (Plate II, fig. 4, and Plate V, fig. 10); to Joyce Townend for Text-fig. 1; and to Anne Stephenson for the remaining text-figures. I must also express thanks to F. W. Moorhouse, E. A. Briggs and P. D. F. Murray for very valuable assistance in the construction and planting out of the "clock-towers" described on p. 117, in which the larvae were reared; and to A. G. Nicholls for the planktonic food-supply which was used during the early stages of the work. The information given as to the breeding-seasons of *Pocillopora* and *Porites* is the result of work carried on partly by myself, but also by S. M. Marshall, who made a large proportion of the collections involved.

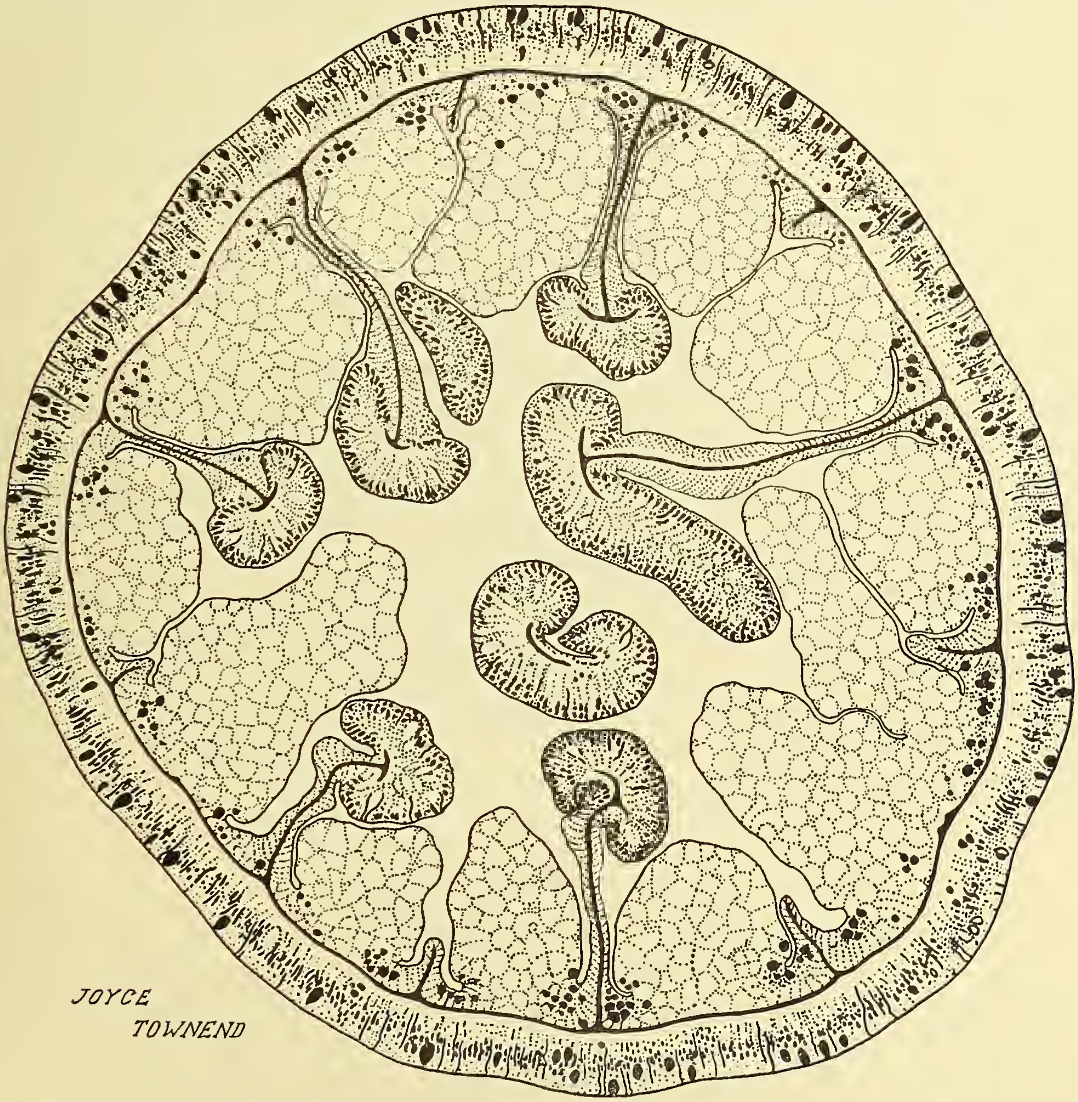
II. *POCILLOPORA BULBOSA.*

A. THE EXTRUSION OF PLANULAE.

This coral (Plate VI, fig. 9) is a branching species common in the moats at Low Isles. It does not, as a rule, attain a very large size; a colony with a diameter of 15 inches may be regarded as a well-grown specimen. The colour of the soft parts during life is usually yellowish brown of several shades, not varying greatly from one colony to another. The polyps expand during daylight (a somewhat exceptional feature), and their tentacles have knobbed tips, the knobs being frequently pale green.

I have not seen eggs or sperm emitted by any colony of this species; but large and well-developed planulae are readily extruded under certain conditions. The emission of planulae in nature is not a continuous process extending over a single breeding-season in each year, but is intermittent, and is related to phases of the moon. The periods of spawning are related to the time of new moon in the summer, and to that of full moon in the winter, with a transition-period in May and June. The evidence for this conclusion will be presented in a later paper on the breeding of reef-animals ; it is incomplete, but sufficient to justify the conclusion stated.

Planulae may be obtained for rearing by breaking off branches of the coral during a breeding-period, and bringing them home in a bucket of sea-water. Many planulae are



Text-fig. 1.—Transverse section of a planula of *Pocillopora bulbosa*, fixed shortly after extrusion. The figure shows the comparatively advanced condition of the free-swimming larva—the specimen in question has already its full complement of mesenteries (six bilaterally arranged couples), three couples of which bear filaments. The endoderm is still in an embryonic condition. × 200.

usually emitted in transit, and others subsequently. They can readily be picked out of the vessel containing the coral, with a pipette, and transferred to finger-bowls for rearing. The first considerable crop observed, from which a number were reared, occurred in December 1928, when some 3,500 were isolated for observation.

The " planulae " (Text-fig. 1) do not deserve their name. They are ciliated, free-swimming larvae, it is true ; but in their internal organization are far beyond the stage to which the term "planula" is strictly applicable among coelenterates. They are, in fact, polyps, but still lack tentacles, and are not yet attached; they have well-developed mesenteries, mesenterial filaments, mouth and throat, and nematocysts of more than one kind. They are large (*e. g.* 1·6 mm. long)—easily visible to the naked eye—opaque cream or light to fairly dark brown in colour, and swim actively in the water at any level in the vessel containing them. The brown colour is due to zooxanthellae within their tissues. Their shape is very variable, both in the same planula and from one to another; but the usual shape is pear-shaped or wedge-shaped, with one end broader than the other. At the narrow end is a spot representing the mouth. Swimming takes place with the aboral end in advance; the forward motion is rapid, and is accompanied by counter-clockwise rotation (viewing the larva from the aboral pole). In some cases the form is so nearly cylindrical that the oral end can only be distinguished by the presence of the mouth. The ectoderm is translucent, the endoderm opaque. The planulae vary considerably in size, although the average is considerably larger than in the case of *Porites haddoni.*

It is a curious fact that any one polyp of the parent colony produces only a single planula at a time, or at most two or three. This is easily verified by studying fertile branches of the coral under a binocular, when the pregnant polyps are easily distinguished, and the contained planulae can be extracted with a needle. The single planula is often nearly as large as the polyp which formed it, when the latter is in a somewhat contracted condition, and fills the whole coelenteron of its parent.

What stimulus causes the extrusion of the planulae in nature we do not know, but the collection of branches, or the changing of the water in which branches already collected have been standing, seem to act as stimuli for their extrusion. Both of these stimuli are of the nature of *disturbances*; it is conceivable that the natural stimulus is the current set up in the moat during certain phases of the ebb and flow of the tide, or the change of temperature which may accompany it.

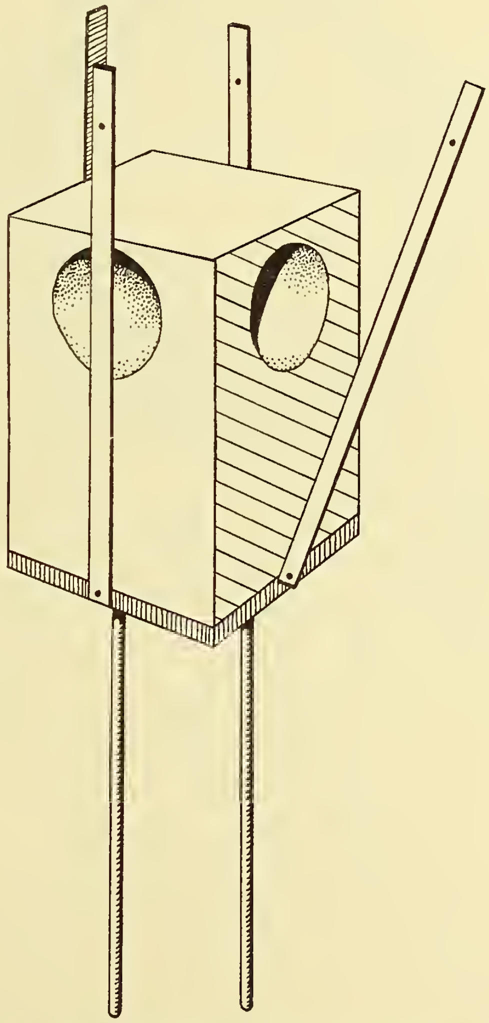
B. THE METHOD OF REARING.

All the young Pocilloporae were reared in finger-bowls, to the inner surface of which they were allowed to attach themselves.* This method was found very convenient, because the bowls were easily handled, and could be placed under a binocular microscope of the type with a long arm, when one wished to study the young corals. After settlement of the planulae had taken place, the bowls were at first submerged in a tank through which sea-water was made to circulate; but later on it was found preferable to plant them out in the sea. The date of birth of the planulae was written on the bowl with a diamond, so that no confusion could take place.

At first the bowls were kept in tanks provided with an arrangement whereby sea-water was allowed to drip into the tank for a certain period of each 24 hours, the excess being carried away through an automatic overflow, so arranged that it removed water from the bottom of the tank. It was not feasible to keep the circulation going throughout

* In some cases young settled colonies showed a tendency to fall off the smooth glass surface of the bowl. It was attempted to correct this by converting the inner surface of a number of bowls into ground-glass, by rubbing it hard with sand, emery powder, etc. This was kindly done for me by Dr. and Mrs. P. D. F. Murray.

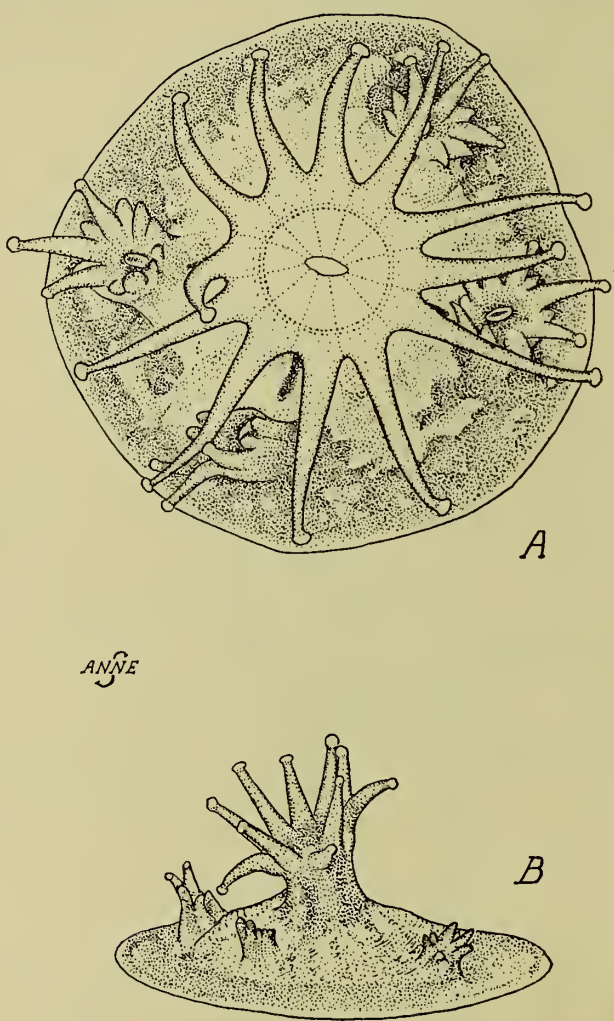
the 24 hours, but this did not appear to interfere seriously with the result. Another method tried was the one worked out by Yonge in the case of his experimental corals: here the water was allowed to well up from the *bottom* of the vessel rather rapidly, causing an overflow at the top, twice during the 24 hours. This method is probably preferable to the first, as giving a more adequate water-change. Whichever method is used, the circulating sea-water should be filtered; otherwise the fine sediment which falls out of



TEXT-FIG. 2.—Diagram to illustrate the structure of the "clock-towers" used for rearing planulae (for description, see text).

suspension becomes too great in amount, and makes it necessary to clean the bowls very often. Both sediment and too frequent cleaning are harmful to the delicate corals.

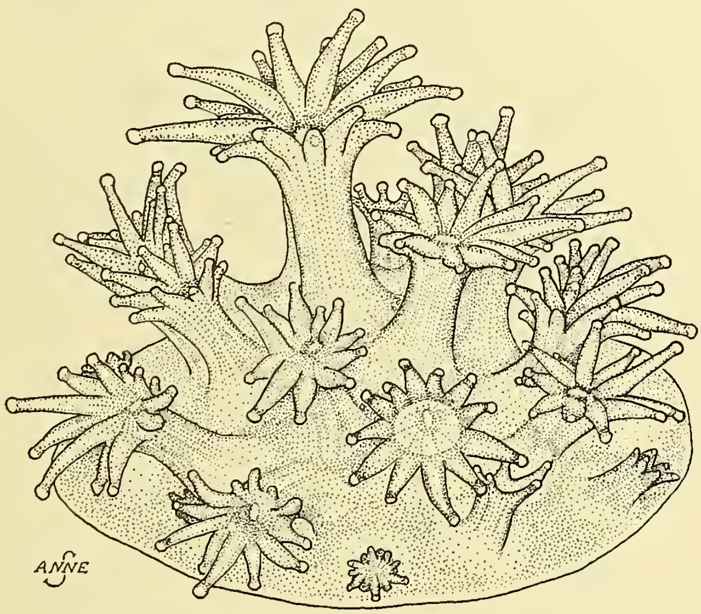
Later on, however, it was found that it is much better to keep the young corals in the sea; and once this had been discovered, they were placed there as soon as settlement had taken place. This was effected as follows: A number of solid tower-like blocks of concrete were constructed, each being about 14 inches high, and 8 × 10 inches in transverse section (Text-fig. 2). They were made in a wooden mould with detachable parts, and before the concrete was poured into the mould, four finger-bowls were so arranged inside the mould that, when the cement had set and they could be removed, each one left a concavity which fitted it exactly, in the cement. The block therefore had the appearance of a small clock-tower with four hollow faces. It also had two long "legs" —two lengths of iron rod about half an inch in diameter and about 2 feet long. Some 6 inches of each rod was inset into the concrete, having been introduced at the time of the



Text-fig. 3.—Young reared colonies of *Pocillopora bulbosa*. A. Colony about 2 weeks 5 days old (counting from date of extrusion of the planula), born on or about 15.xii.28; viewed from above. The colony consists of a single primary polyp and 4 buds. The pale irregular area round the primary polyp represents the thickened part of its skeleton, as seen through the living tissue. The skeletons of the buds have begun to form, and have modified the shape of the thickened part of the skeleton of the primary polyp. B. Colony about 2 weeks 6 days old, born on or about 14.xii.28; viewed from the side. This colony has one primary polyp and three buds, and is slightly less advanced than A. Note the central mound caused by the thickening of the skeleton in this region, and the flat peripheral area. Fig. A, × 20; fig. B, × 16.

making of the block; the remaining 18 inches projected from the bottom of the block. These towers were planted out in the sea, some in the western moat and others in the anchorage, in pools which would retain enough water to cover them at all states of the tide. They were kept in place by the two legs, which were driven into the reef, a hole having previously been made for each with a large crowbar. In each of the four cavities in the block a finger-bowl was placed. It was prevented from falling out of the hollow by a wooden lath passing vertically across its mouth, up the middle of the side of the block. The four laths were attached, each by a single nail, to a square of thick wood which lay underneath the block, and which was perforated by two holes through which the " legs " passed. This meant that each lath would swivel on its nail, and could be pushed aside when one wished to remove the bowl which it guarded. Between the inspections of the bowls, the four laths were tied together with string or wire passing through holes in their upper ends ; these upper ends projected above the top of the block.

To anyone who may try this method in the future, the warning should be given that before the cement is poured into the mould, round the finger-bowls, each finger-bowl should be coated as smoothly as possible with thoroughly greased newspaper, and two pieces of string should be placed round the back of it, with the ends projecting, in order

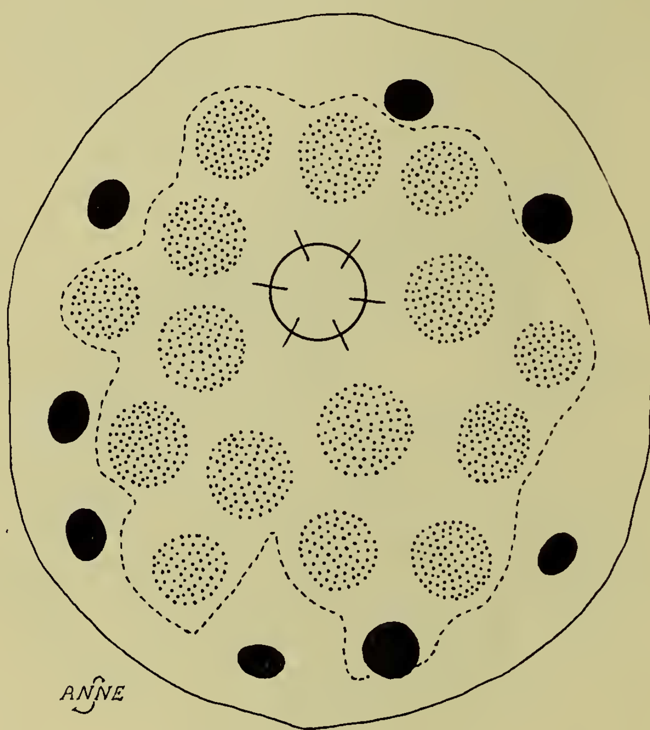


TEXT-FIG. 4.—Side view of the most advanced colony of *Pocillopora bulbosa* reared from a single planula in a finger-bowl. A plan of this colony is reproduced in Text-fig. 5. The planula was born on 14.xii.28, and the drawing made 10 weeks and 5 days after its extrusion. The skeleton does not show at all here, as the coenosarc is raised well above it. × 17.

to facilitate pulling it out afterwards. Even with these precautions it may have to be extracted by breaking it. Further, the " clock-tower " must soak in the sea for some time before use, so that the concrete may be " cured " ; otherwise the substances which dissolve out of it may affect the young corals. Three weeks is a safe period for the curing process, but probably somewhat less is actually sufficient.

This method of rearing has several advantages. First of all it enables the young corals to catch plankton for themselves, and overcomes the difficult problem of feeding them artificially. Secondly, it exposes them to approximately natural conditions, and they respond to this by more rapid and normal growth. Thirdly, they require under these conditions very little attention, and need only be visited periodically, so that the bowls may be gently rinsed to prevent too great an accumulation of fine sediment. The bowls are, of course, placed on one side in the tower to prevent the accumulation of too much sediment—if they were fixed right way up the corals would be smothered by collecting sediment in a short time. It is also important that the bowl should be near the top of the tower—*i. e.* raised some inches above the sand of the pool—otherwise the danger from moving sand and accumulating sediment would be too great. The presence of the lath across the mouth of each bowl did not appear to interfere with the circulation nor to prevent the entry of an adequate amount of food and light. The method, at any rate, proved very successful.

Before the corals were placed in the sea they were fed as follows: When very young they were given small amounts of a culture of protozoa made by keeping some leaves of

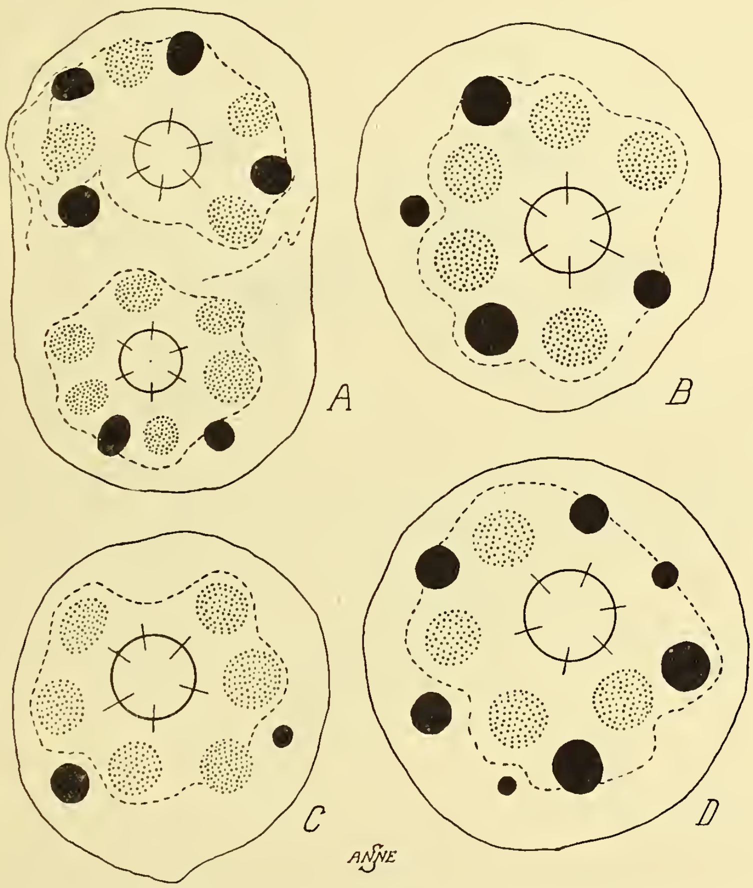


Text-fig. 5.—Plan of the colony represented in Text-fig. 4, drawn 10 weeks and 6 days after extrusion of the planula. The primary polyp is represented by a circle, the six rays indicating the positions of the principal septa. The older buds, of which there are 15, are stippled; the younger ones, 8 in number, are represented in black. The dotted line indicates approximately the edge of the thickened central part of the skeleton. × 17.

Thalassia and a little organic detritus in a separate finger-bowl. The *Thalassia* leaves prevent excessive decay in such a culture, but permit the life of protozoa. Later on, the corals were given freshly-caught plankton from which the larger organisms had been filtered out. How far the corals benefited from this feeding it is impossible to say, but at least they continued to grow. I think, however, they would not continue healthy beyond a certain point unless kept in the sea; moreover, the fall of sediment, even from filtered water, in an aquarium tank, is of a sticky and insidious nature, and not easily removed without damage to the corals. It is clear, both from the tank-rearing and the outdoor-rearing that fine sediment is a serious enemy to young corals.

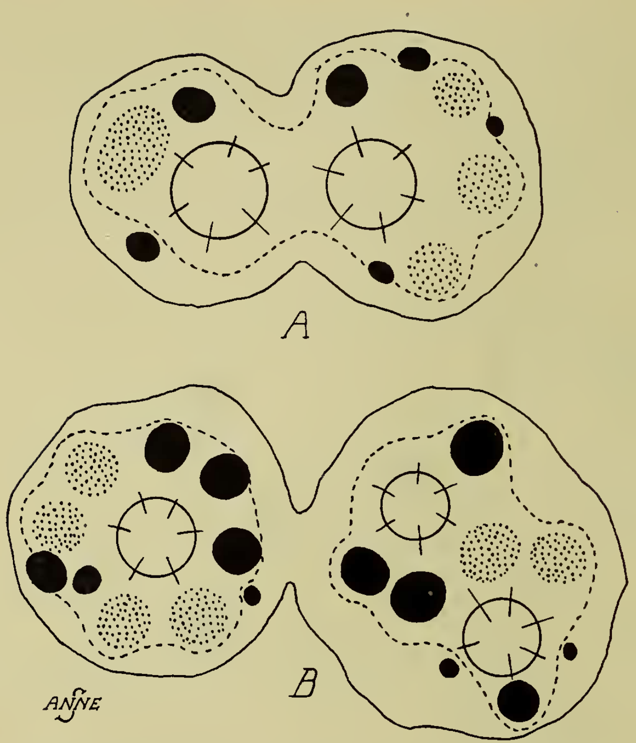
The keeping of planulae *before* they have settled is more troublesome than afterwards. It is essential to change their water every day, and this can be done by running off the water through a glass tube covered at its submerged end by a flattened bag of bolting-silk, to the surface of which the planulae adhere. This is not, however, a very safe method, and may result in fatalities. A better way is to remove each planula to clean water with a pipette ; but this is very tedious.

A large amount of material was preserved for detailed study later. Some of the attached polyps or colonies were fixed in neutral formalin (so preserving both skeleton



Text-fig. 6.—Plans of young reared colonies of *Pocillopora bulbosa*, illustrating the arrangement and order of appearance of the early buds. The conventions adopted are as in Text-fig. 5. A. Colony 7 weeks 6 days old, born 15.xii.28 ; formed by fusion of two primary polyps, and subsequent budding. The colonies figured in B, C, and D, were each formed by budding from a single primary polyp, and were born on same date as A. C and D were the same age as A ; B was one day older, at the time of drawing. Note that the primary circle of buds consists of 4, 5, or 6 buds. Magnifications similar to those of Text-fig. 7.

and soft parts), others in Bouin's fluid, which, of course, decalcifies them ; in either case they were transferred for storage to 70% alcohol. The fixation, especially by means of Bouin, has proved to be excellent. Free-swimming planulae were fixed either in Bouin or Champy. Skeletons were prepared by gently pouring a hot solution of KOH (10%) on to the young corals ; this removed the tissue easily in most cases (sometimes it had to be done more than once), and did no damage to the delicate skeletons, which were afterwards well washed.



Text-fig. 7.—Further plans of young reared colonies of *Pocillopora bulbosa :* conventions as in figs. 5 and 6. A. Colony formed from fusion of two primary polyps, and subsequent budding. A case in which two semicircles of buds have been formed, on the sides of the primary polyps which are turned away from each other, no buds having appeared between the two. Age of colony about 7 weeks, extrusion of planulae on or about 15.xii.28. B. Colony formed by fusion of 3 primary polyps, and subsequent budding. In the right-hand half of the colony budding is irregular, and buds have appeared between the two primary polyps. Age of colony about 6 weeks 4 days, extrusion of planulac on or about 15.xii.28. A, × 16; B, × 12.

C. THE DEVELOPMENT OF THE COLONY AFTER THE ATTACHMENT OF THE LARVA.

The fixation of the planula sometimes takes place within 24 hours after its extrusion ; in other cases it does not occur for two or three days, or for a week or more. How long the free-swimming period lasts, in the sea, I cannot tell, but I suspect that it is short. Planulae in captivity tend to settle within a few days of extrusion, or else appear disinclined to do so at all ; such as had failed to do so after about ten days in captivity were usually preserved, as they no longer seemed normal.

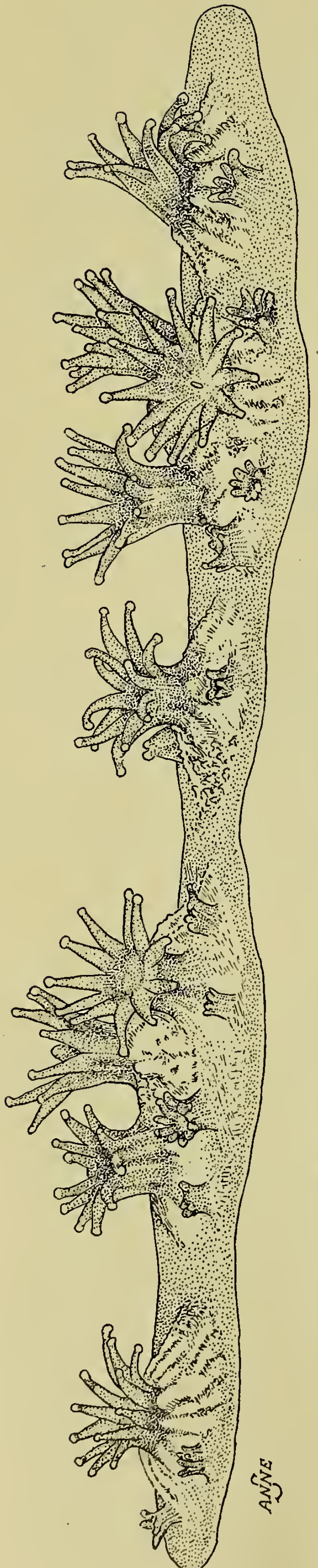
This disinclination to settle may have been due to premature extrusion of a proportion of the planulae, as a result of the disturbance caused to the parent branches by collecting them ; had the branches been left undisturbed in the sea, such planulae might well have remained longer in the coelenteron of the parent polyp. This perhaps accounts for part of the number which fail to settle ; but against it must be put the consideration that many of the planulae which do not settle appear to be stout and well-developed individuals. This suggests rather that unless they settle fairly soon in captivity, their condition becomes in some way pathological, although they do not appear actually unhealthy. Before a planula settles definitely, it may attach itself temporarily to the substratum, and become dome-shaped ; but will afterwards swim away again, and resume its ordinary form.

I suspect that the planulae, during their brief free life in the sea, often remain near the bottom and are not carried far afield. A tow-netting was taken by S. M. Marshall and myself on a day when *Pocillopora* was known to be fertile (and when planulae could be obtained by picking branches), right round the moat, and only a foot or so above the coral. Not a single planula was captured. This must mean either that any planulae recently extruded had been swept away, or that they were actually among the coral near the bottom; or that few had been extruded although the parent colonies were fertile. In the regular tow-nettings taken by Russell and Colman coral planulae were of notably rare occurrence. They were not found in any of the hauls taken over the reef-flat; and at the plankton station three miles from the reef they were taken only on three occasions

TEXT-FIG. 8.—A young living colony (reared) of *Pocillopora bulbosa*, viewed from above. The colony was formed by fusion of 8 primary polyps, and subsequent budding. The 8 planulae were extruded on or about 15.xii.28, and the colony was about two weeks old at the time of drawing. One of the primary polyps is contracted. Nine buds have appeared. × 12.

(14th, 19th and 27th December, 1928), and only once (14th December) in quantity. A certain number of planulae, probably belonging to *Acropora*, were obtained by S. M. Marshall from tow-nettings in the anchorage on 24th, 26th and 27th December, 1928.

When the planula definitely settles down and becomes firmly attached it becomes apparently much larger, because it spreads out flat and becomes thin and coin-like, an attenuated disc with a slight mound in the centre, and with a diameter of 1·7–1·8 mm. or more. It begins to secrete skeleton almost at once; so rapidly, indeed, that one rarely catches a polyp which has settled but which has no skeleton. The appearance of a normal polyp shortly after settlement is illustrated in Plate I, fig. 2. This shows the disc-like form, the central mound bearing the small mouth with its narrow pale-green lip; no tentacles have yet developed, but the skeleton is well formed; the thin basal plate is clearly visible round the edge of the polyp, where it projects beyond the tissues of the latter,



Text-fig. 9.—A young reared colony of *Pocillopora bulbosa*, viewed from one side. It consists of 9 primary polyps, which have fused, and a number of buds, of which 12 are visible. Age of colony about 2 weeks 4 days, planulae extruded on or about 14.xii.28. × 13.

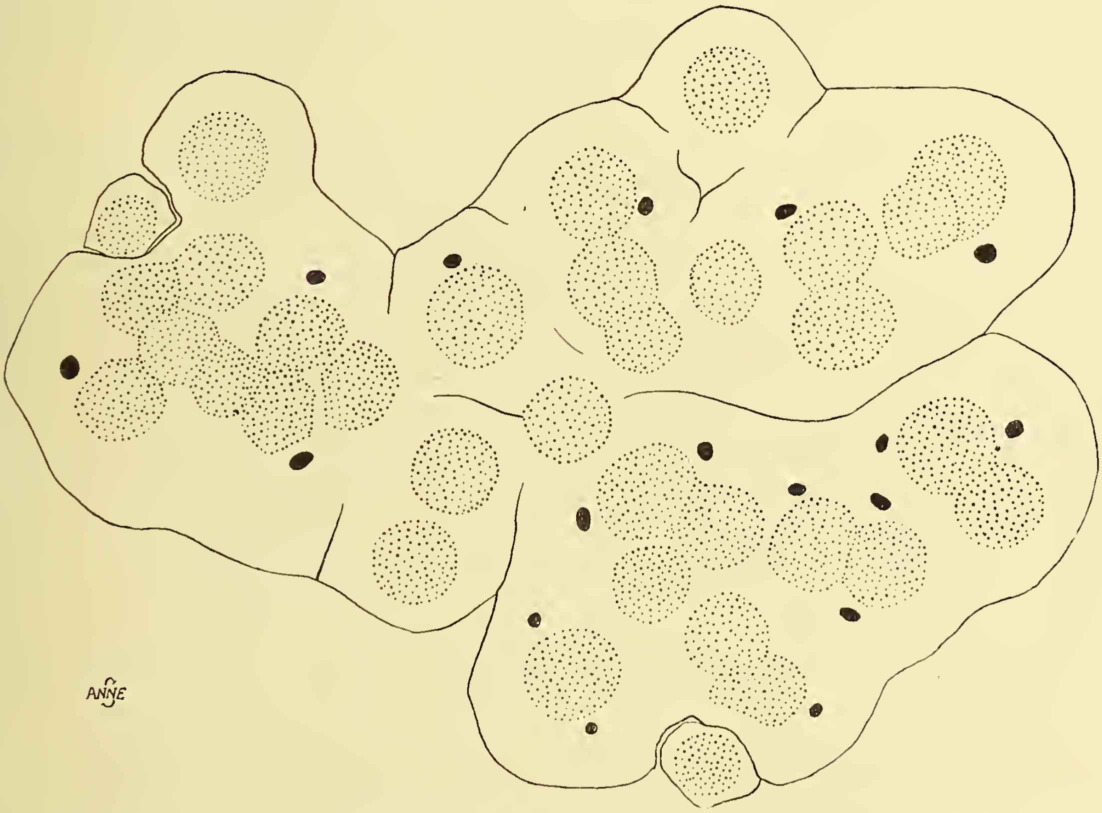
or is covered by a very thin membrane only; there are 24 septa (in three alternating cycles), visible as white rays through the outer part of the polyp's tissues; and the body of the polyp has 12 radial cream-coloured stripes, 6 principal and 6 subsidiary.

It happens fairly often that for some reason a planula which has become more or less flattened fails to settle; it may become entangled in the surface-film, or may for some other reason fail to attach itself. But, in spite of this, it may begin to form a skeleton, which, as a result of the non-attachment of the larva, has not the normal form, and may be considerably distorted. Once this skeleton has started, in the majority of cases the larva has no longer any chance of attaching itself, and is bound to die sooner or later. This state of affairs suggests that the stimulus to form a skeleton is an internal one, which may come into action at a given time, even in the absence of the additional stimulus which, in a normal case, is supplied by contact with the substratum. Presumably, in a normal case, both stimuli may be effective. These unattached polyps may also develop tentacles.

The tentacles of the normal polyp begin to grow out as small papillae very soon after settlement; in some cases they are discernible within 24 hours of fixation, and in a few days they attain full size. They appear approximately simultaneously, and normally grow at about the same rate; so that the polyp, when fully formed, has 12 tentacles, arranged in two cycles, 6 exocoelic and 6 endocoelic, the endocoelic ones being a little the longer. If any other unevenness in the lengths of the tentacles appears, it follows no systematic plan. This is in sharp contrast to the development of the tentacles in buds, which, as will be seen later, takes place in a different manner.

Before describing the development of the colony, we must notice a curious feature which has already been described by Boschma for *Meandra areolata*, and by other authors for other corals. Under the conditions of rearing which prevail in a finger-bowl, a rather large number of settled polyps may be living together in a small space; this is accentuated by the fact that they have a tendency to settle particularly thickly just beneath the water-line, and also round the groove where the sides and bottom of the bowl meet. As a consequence, if two or more polyps settle very close to one another, they soon grow, increase their area, and come into contact with one another. As soon as this happens, they fuse ; and the fusion becomes so complete, both as regards flesh and skeleton, that the independent organisms become one. Therefore, colonies are formed at this stage, not by budding or by fission, but by the fusion of independent primary polyps. A number of these fusions are illustrated in the accompanying plates and text-figures, the details of each example being explained in connection with its figure.

After a period* during which the primary polyp or polyps simply grow and add to their skeletons, budding begins. This will be described first in the typical case, *i. e.* in the case of a single polyp which has not fused with any others, and which can



TEXT-FIG. 10.—Plan of a young reared colony of *Pocillopora bulbosa*, formed by the fusion of 32 primary polyps and the subsequent production of 17 buds. Two other primary polyps have nearly fused with the main colony. All the buds were in a very young condition at the time of drawing. Age of colony about 2 weeks 6 days, extrusion of planulae on or about 15.xii.28. × 9.

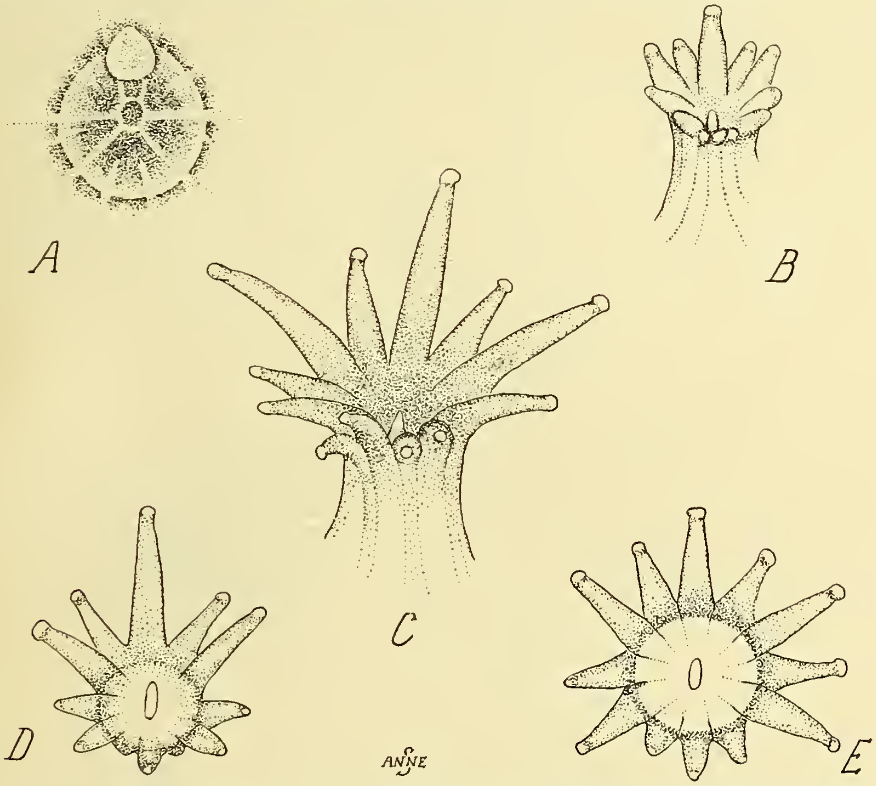
therefore develop unfettered. The story briefly is this : there appears first, round the base of the primary polyp, a single circle of buds (which do not usually appear simultaneously) ; after these have undergone a certain amount of development a second circle appears, alternating more or less regularly with the first, and placed further out from the primary polyp ; and so on. The development of these successive circles is not, however, perfectly regular, and tends to become less so with age. The first circle may consist of

* I have not given details as to the exact times after the extrusion of the planulae at which the various stages are reached, because these times vary too much, according to circumstances, to have much significance in a summary statement. But the age of each stage figured, wherever known, is stated in the explanations of the plates and text-figures, so amplifying the text. This point will be further elaborated later.

6 buds, more or less evenly spaced out ; but almost equally often it consists of 4 or 5, and sometimes of 3 or of 7 ; these buds may be fairly evenly or distinctly irregularly placed. As growth proceeds there is a tendency for the number of buds on one side of the colony to become greater than on the other, so that it loses its original symmetry. During the early stages, therefore, the colony grows out laterally, retaining its disc-like form, but increasing its area. At the same time, while this budding has been going on, the skeleton has been increasing in thickness in its central parts ; from a very early stage the central region has assumed the shape of a low mound. The thickening affects, at first, only the calyx of the primary polyp but soon spreads further afield. (This thickening-up of the skeleton tends to take place less markedly in colonies reared in finger-bowls than in those which have developed naturally in the wild.)

After a time the colony has reached the condition illustrated in Plate III, fig. 4, in which it forms a thickened, irregular disc with numerous corallites derived by budding from a single parent ; it shows as yet no branched structure. The figures on Plate VI illustrate the transition from this condition to that of the adult colony. In fig. 1 the colony has become conical ; in fig. 2 a definite upward-growing branch has appeared ; in fig. 3 the branch has subdivided. In figs. 4 and 5 several branches have grown out independently from the basal expansion ; and in the remaining figures intermediate stages between a colony with a single branch or with a few simple branches, and the adult many-branched condition, are illustrated. The figures on this plate were obtained as follows : The most advanced colony reared *in a finger-bowl* is that illustrated in Text-figs. 4 and 5, and in Plate III, fig. 1. The stages shown in Plate VI, figs. 1–3, were obtained by planting out logs of wood in the Madrepore moat ; and a number of other similar ones were procured by planting out other materials (pieces of clean beach sandstone, clean dried clam-shells, pieces of drain-pipe, etc.) in various positions on the reef. These materials were fastened down so that they could not move, and a number of planulae of *Pocillopora* and other corals settled upon them during the course of the year. The exact age of the colonies so obtained is, of course, not known ; but since the dates of planting out each deposit of materials and those of the collection of each young colony are known, any such colony is younger than the interval of time between the setting out of the materials and the collection of the young coral. The remaining figures on Plate VI are from a series of colonies collected on the reef, but are of unknown age. The outline of development just given refers, of course, to typical cases ; a number of aberrant or exceptional examples are, as always, to be found, but these will be dealt with in Part II.

So much for the course of events in a colony founded by a single polyp. In the case of colonies formed by fusion, the early development is somewhat modified, but after a certain point the procedure must be much as in the normal case. The early modification is due mainly to the fact that in a compound colony, unless the calices of the primary polyps are sufficiently distant one from another on the common basal plate, a ring of buds cannot develop freely round each, and the production of buds becomes to a greater or lesser degree irregular. If the calices of two or more fused polyps lie very close together (actually in contact), buds do not, in any case I have seen, develop between them, but only round the sides which are turned away from each other, or in the angles between them ; *i. e.* the fused polyps form a nucleus about which buds will develop. If however, there is any space between the primary polyps, even quite a narrow one, buds may develop between them ; but this does not always happen, since sometimes, even when the interval is considerable, no buds arise from it during the early stages, but develop in semicircles round the sides of the primary polyps which do not face each other. This applies only to early stages, however ; as soon as the first branch begins to appear, new buds develop, in the growing region, between very close-set calices.

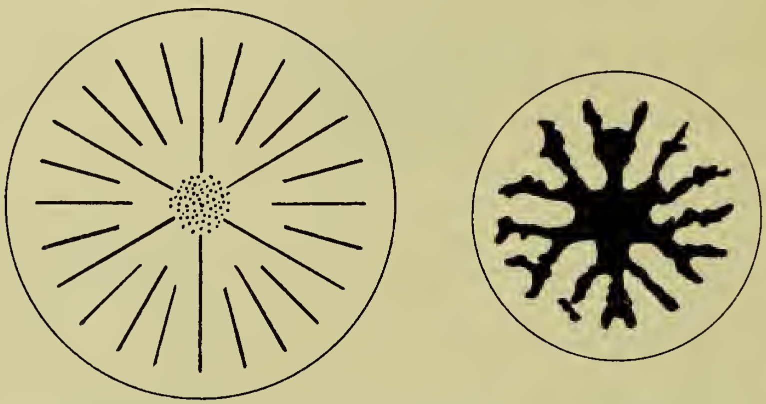


TEXT-FIG. 11.—A series of buds of *Pocillopora bulbosa*, much enlarged (A being more magnified than the others), to illustrate the symmetry of the buds and the development of their tentacles. All the figures are similarly oriented—*i. e.* the lower side of each figure represents the side of the bud which faces the primary polyp or the centre of the colony ; vertical lines drawn through the centre of each figure would therefore represent approximately radii of the colony. A, very young bud with one short directive-tentacle only ; the mouth is formed, and the 6 couples of mesenteries are visible because of the transparency of the tissues. The other figures illustrate the bilateral appearance of the tentacles, in couples symmetrical about the directive axis ; the dominance, maintained for some time, of the first directive-tentacle to appear : and the shortness of the tentacles on the side of the bud which faces the centre of the colony.

Lastly, the development of the buds themselves may be considered ; it is illustrated in Text-fig. 11. The bud when first seen consists of a small mound, which rapidly attains the stage illustrated in fig. A, in which not only the mouth, but also the mesenteries and a single short tentacle are visible. This tentacle is always the first to appear, and it is *the directive tentacle farthest away from the primary polyp of the colony.* In other words, the bud, at the present stage of its life, is *bilaterally symmetrical about its directive axis, and its directive axis coincides with a radius of the whole colony.** This markedly bilateral

* This applies strictly, of course, only in the case of radially symmetrical colonies, *i. e.* those derived from a single planula, and is subject to the reservation that the coincidence between radius of colony and directive axis of bud is sometimes approximate rather than exact. In colonies formed by fusion, the buds arise with as nearly the typical orientation as circumstances permit.

phase is maintained for a long time. The remaining figures, B–E, show how the rest of the 12 tentacles develop—in couples, of approximately the same length in each couple, one member of each couple being placed on either side of the directive axis of the bud, *i. e.* on either side of a radius of the colony. The long axis of the mouth corresponds, of course, with the directive axis; and the oral disc tends to be oval, the longer axis at right angles to the directive axis. It is further apparent from these and some of the other figures, that the tentacles on the side of the bud *nearest the primary polyp* are shorter than the rest, and this condition also persists for a long time. It has the effect, in the whole colony, of making an even web of tentacles (Text-fig. 4), covering the whole surface, when the polyps are expanded; the short inner tentacles of the buds do not interfere either with the long outer tentacles of any buds more centrally placed than themselves, nor with those of the primary polyp; and between the buds and the primary polyp much of the available area is covered.



TEXT-FIG. 12.—Diagrammatic representation of the skeletons of young polyps of *Pocillopora bulbosa* (left-hand figure) and *Porites haddoni*. Both figures are to the same scale (× 20). The *Pocillopora* was drawn from a skeleton about 5 weeks 6 days old, the planula extruded on or about 14.xii.28. The *Porites* was from a specimen 7 days old (planula extruded 7.ii.29). The polyp belonging to this skeleton had its tentacles at the stage represented in Text-fig. 13, B. The finer detail is not represented in this figure, since the skeleton was drawn as seen through the flesh of the polyp. (The specimen of *Pocillopora* used for this diagram was unusually backward in development for its age.)

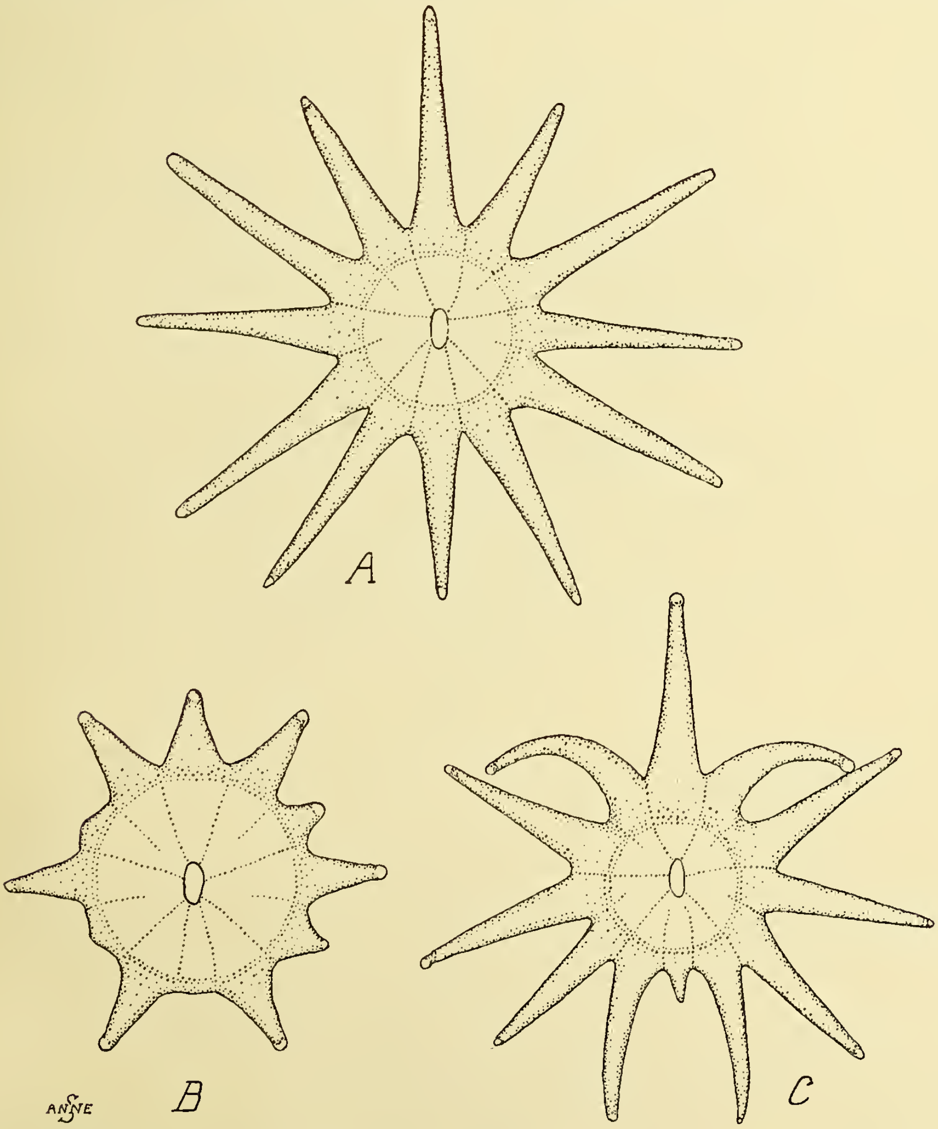
D. THE PROGRESSIVE MODIFICATION OF THE SKELETON.

To what has already been said it is necessary to add that the outline of skeletal development is as follows: At first the septa are independent ridges on the basal plate (Text-fig. 12, Plate II, figs. 1 and 6); later on they fuse and form a raised corona or calyx (Plate II, figs. 2–4). In the early stages of calyx-formation the six principal septa meet or nearly meet (in a typical case) a central columella. In cases which appear to be atypical, there may be a ring-like skeletal structure in the centre, instead of a columella; and other variations. Both the calyx and the plate become prickly. The skeleton of a primary bud has at first six conspicuous primary septa and a columella. As development proceeds, the coenenchyme between the corallites becomes thickened (Plate III, figs. 1 and 4). When the colony begins to form branches, the shape of the newly-formed corallites is different from that of the earlier ones (Plate VI, figs. 1–5); and as a branch grows upwards, the proximal calices became different from the distal ones. The details will be described in Part II.

III. *PORITES HADDONI.*

A. THE EXTRUSION OF PLANULAE.

The species of *Porites* which provided the planulae for rearing was common in the Low Isles moats. It was one of the massive forms, without branches or actual lobes, the



TEXT-FIG. 13.—The arrangement of tentacles in primary polyps of *Porites haddoni*. B, in a polyp 7 days old (planula extruded 7.ii.29); here only 11 of the 12 tentacles have appeared, 4 are still very short, and the bilateral arrangement is very marked. The mesenteries are indicated by dotted lines. The central ray of the trident in the skeleton (Text-fig. 12) corresponds to the directive endocoel which has not yet developed a tentacle. C, in a polyp 7 weeks 4 days old (planula extruded 7.ii.29); here the tentacles are longer, but the bilateral arrangement is still marked; the curious curvature of the tentacles shown is habitual in some polyps. A, in a polyp of the same age as C, born the same day and reared in the same bowl, but in which the tentacles have attained a more radially symmetrical condition; traces of bilateral symmetry still remain. Fig. B is magnified 32 diameters, the other figures considerably less.

surface being at most irregular or nodulated. The majority of the planulae were obtained from young colonies, since these are easier to collect than large ones, besides which they seemed more ready to extrude planulae. The colour of the colonies varied from cream or pale fawn to yellowish or purplish. I speak of the coral in question as *Porites haddoni* ; but it is not impossible that more than one species provided us with planulae. The identification of *Porites*, down to a species, is probably impossible in the field ; and in any case there is no real certainty as to what characteristics constitute specific limits in the genus, the matter being still within the realm of personal opinion. We can only say that our specimens were derived from a common habitat ; that they may well have belonged to a single species ; and that the development of their planulae presents a coherent story with no suggestion of specific differences in ontogeny.

The first planulae observed from *Porites* were found by Yonge in an aquarium tank on 26th January, 1929. From that time onwards *Porites* were brought in from the reef every few days, until 22nd July. The production of planulae went on all the time. In this case the breeding appeared to be continuous, with no suggestion of periodicity, but the number produced fell off greatly in June and July. The details of this spawning, as in the case of *Pocillopora*, will be recorded in the report on breeding of reef animals.

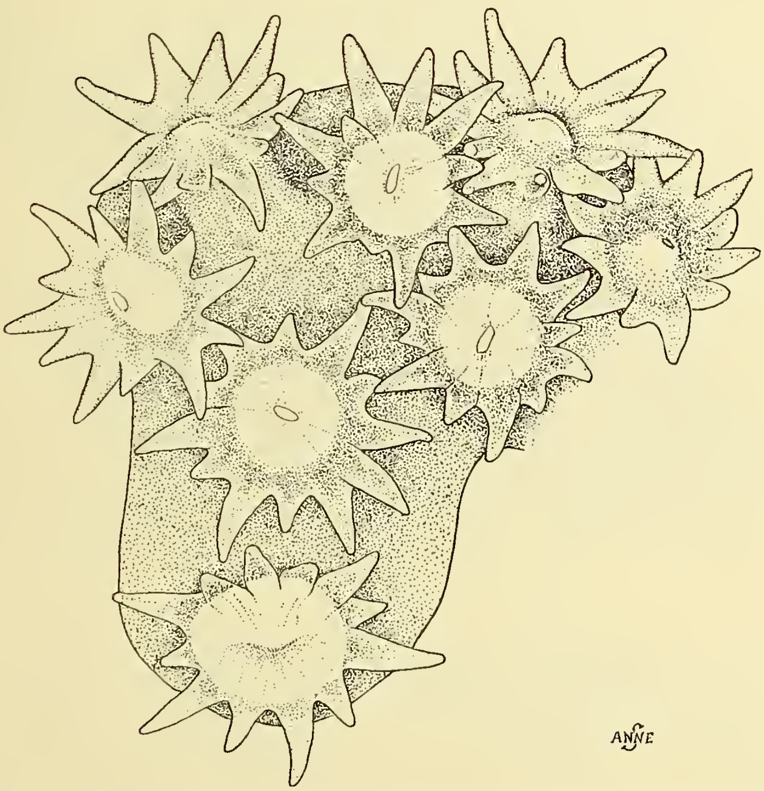
The method of obtaining the planulae was the same as in *Pocillopora*, by bringing in colonies in a bucket. The rearing also followed the same plan, but that in one case some planulae settled in a small tank, and this was planted out in the sea, on end, in a special cement tower of its own. In the case of *Porites* the finger-bowls were all put out in the sea as soon as the planulae had settled, none of the latter being reared under aquarium conditions. The planulae of *Porites* are smaller than average planulae of *Pocillopora*, and paler in colour ; otherwise they call for no further comment in this part of the paper.

B. THE DEVELOPMENT OF THE COLONY AFTER THE ATTACHMENT OF THE LARVA.

The general outline of the early stages is the same here as in *Pocillopora*, with certain sharp differences of detail. I can say nothing about the way in which the successive buds arise in this case, because although my colonies produced a large number of buds, they grew rather slowly, and had not time to produce more than an initial number while they were under observation. Moreover, I had a considerable proportion of fusion-colonies, and fusion always complicates the arrangement of buds.

The skeleton of a young *Porites* polyp is very different from that of a young *Pocillopora*, consisting, apart from the basal plate, of a series of irregular radial elements, which from an early age have the bilateral arrangement shown in Text-fig. 12. When fusion takes place, as it does very readily and on a large scale, the skeletons (but not the soft parts) of individual polyps may lose their identity altogether, and become lost in a confused tangle of lace-like trabeculae (Plate IV, fig. 1).

The development of the tentacles in the settled larva of *Porites* is also unlike that of *Pocillopora*. Instead of growing out approximately evenly, they have a strongly-marked bilateral arrangement from the very beginning (Text-fig. 13, B), and even when they become long and more equal in length, traces of the bilateral condition usually still persist. The number of tentacles is normally 12, but sometimes other numbers (10, 18, etc.) occur. Another peculiarity is this—that in a fusion-colony consisting of a number of primary individuals, those round the edge tend to grow longer tentacles on the side which is turned away from the middle of the colony than on the side turned towards the middle. This means that they grow longer tentacles on the side where these can stretch out freely without coming into contact with the tentacles of adjacent polyps ; there is no constant relation



TEXT-FIG. 14.—Part of a colony of *Porites haddoni* formed by the fusion of 19 primary polyps, of which 8 are shown. No budding has yet taken place. Age of colony 7 days ; planulae extruded 7.ii.29. × 20.

here between the lengths of the tentacles and the directive axis. A colony of this description, therefore, repeats to some extent the state of affairs found in a colony such as that illustrated in Text-fig. 4 ; but in this case it is not *buds* which have long outer tentacles, but primary polyps. Inequality of the tentacles of primary polyps, in this sense, is sometimes seen in *Pocillopora* in a less marked degree.

The development of the buds in *Porites* follows that of the buds of *Pocillopora* very closely—*i. e.* a single directive tentacle appears first, on the side of the bud farthest from the centre of the colony, and the remaining tentacles develop bilaterally about the directive axis of the bud, which coincides more or less closely with a radius of the colony. The tentacles on the side nearest the centre of the colony remain, as before, shorter than the others for some time.

Text-fig. 15.—Part of a colony of *Porites haddoni* formed by the fusion of 19 primary polyps. The tentacles have become longer than in Text-fig. 14, and the tendency of the marginal polyps to develop long tentacles on the side of the polyp turned away from the centre of the colony is clearly illustrated. Two buds (visible as knobs without tentacles) are present. Age of colony 7 weeks 6 days ; planulae extruded 7.ii.29. Magnification somewhat less than that of Text-fig. 14.

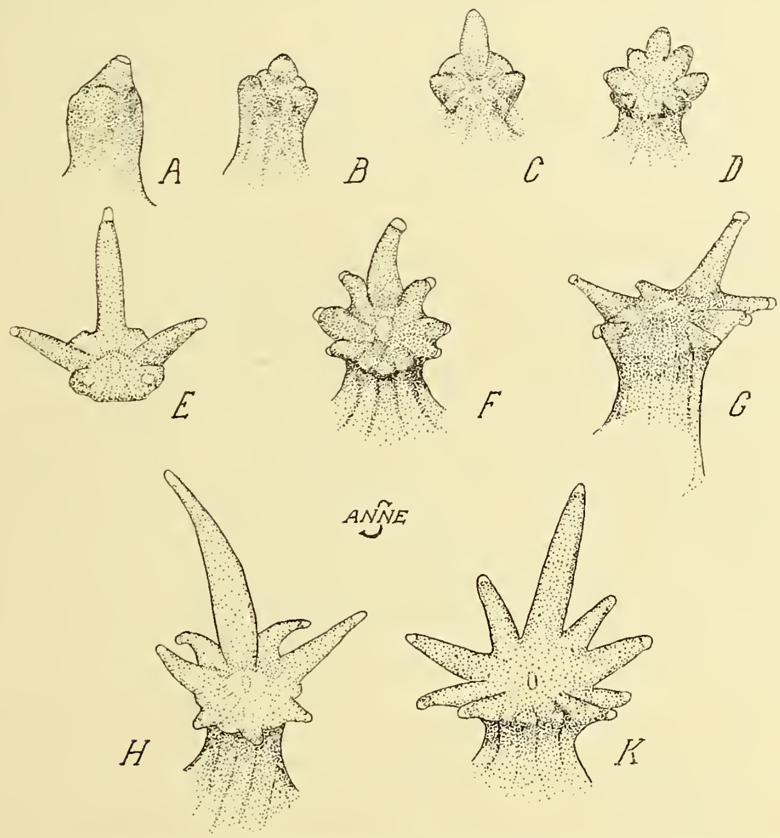
IV. THE RESPONSE OF YOUNG COLONIES TO SEDIMENTATION.

In the photographs of young skeletons reproduced in the plates, both in those of *Pocillopora* and in those of *Porites*, it will be noticed that certain of the young colonies have a raised rim, sometimes broad and incurved, either round the margin of the basal plate, or in some more central position. These rims are, I believe, a response to accumulations of fine sediment, matted together by a microscopic growth of algae, which frequently form round the edges or even upon the surfaces of young corals. That the rims are a response to certain conditions in the environment, and are not a necessary part of the corallum, constituting a specific characteristic, is suggested by the following considerations :

1. In both *Pocillopora* and *Porites* the rims in question are present only in certain individuals. That the rimless condition is normal and healthy in *Pocillopora* I feel certain. In *Porites* a well-developed rim is very often present, but this coral has a very small polyp,

more easily subdued than that of *Pocillopora*, and may well need to react more strongly. When working on the living material, I gained the impression very distinctly that the absence of a rim was the more normal and healthy condition, and that the rim was put up to keep off deleterious substances from damaging the delicate flesh at the edge of the colony.

2. The mode of occurrence of the rims, when they are present, is erratic. In fusion-colonies of *Porites* (Plate IV, fig. 1 ; Plate V, figs. 5–9, 11) these rims may or may not occur between the fused corallites. This should not be the case if the presence of the rims is a



Text-fig. 16.—A series of buds of *Porites haddoni*, illustrating the form and orientation of the bud, the predominance during the early stages of the first directive-tentacle to appear, and the bilateral appearance of the other tentacles. The figures are oriented as in Text-fig. 11, and are much enlarged.

specific feature. Moreover, a rim is often present in one part of the circumference of a colony, absent in another part. Again, there may be two rims (complete or incomplete), one inside the other ; or a single rim at the edge, or a little way in from the edge.

3. In a number of colonies the rim does not occur either at or near the edge, as it should if it were a regular morphological feature. A particularly good example of this is shown in Plate III, fig. 6, which represents a colony of *Pocillopora* with an irregular rim surrounding the white central part of the colony only. In this colony, at the time when it was fixed, the central part (clean and white in the skeleton) was alive and healthy ; but the peripheral part, outside the rim, was dead, and was matted with the algae and sediment which had killed it. Another such colony is shown in fig. 7 of the same plate, and here the living

parts of the colony, at the time of fixation, were limited to two small areas including the two primary polyps—these areas are just distinguishable in the figure, each with its surrounding ridge. Such instances are plentiful, and the protective ridges thus formed often cut right across the corallite of a dead or half-dead polyp (as in fig. 7, on the right).

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DESCRIPTION OF PLATE I.

(*In this and the following plates the magnifications are given exactly or to the nearest whole number; they are calculated from diameters. The same applies to the text-figures.*)

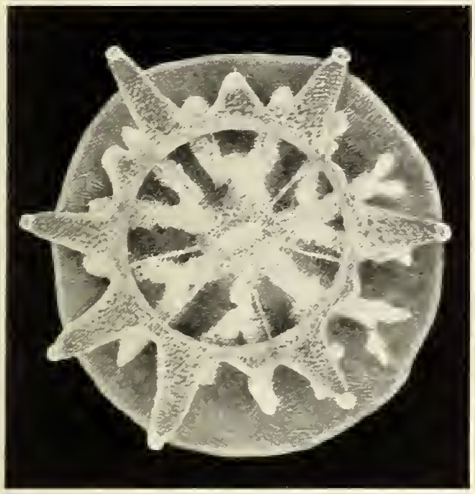
Fig. 1.—A polyp of *Porites haddoni*, 7 days after the extrusion of the planula, which occurred on 7.ii.29. The tentacles are still in an early stage of formation, and are bilaterally arranged. The skeleton is partially visible through the translucent tissues. × 35.

Fig. 2.—A very young polyp of *Pocillopora bulbosa*, which had been settled for at least a day. It has not yet developed tentacles, but has a mouth, a basal plate (projecting a little beyond the tissues of the polyp), and 24 septa in three cycles (visible as white radial streaks through the flesh of the peripheral part of the polyp). The central part of the polyp is mound-shaped, and has radial bands of cream-coloured pigment, in two cycles. Drawn 17.xii.28. × 23.

Fig. 3.—A young colony of *Porites haddoni*, consisting of 4 polyps, of which probably two are primaries and two are buds; they are shown in a contracted condition. The colony was about 4 weeks old, the planulae being extruded shortly before 5.ii.29. × 30.

Fig. 4.—A young colony of *Porites haddoni*, formed by the fusion of 3 primary polyps, which are here shown fully expanded, so that the skeleton is completely concealed. The colony was 5 weeks and 2 days old, the planulae being extruded on 7.ii.29. The colony also possessed a small polyp (hidden in the drawing by one of the larger ones) which was probably a bud. × 13.

Fig. 5.—A young colony of *Pocillopora bulbosa*, viewed from above. The colony consists of a single primary polyp surrounded by 9 buds. The calices of the buds are well formed, and are fused with that of the primary polyp; the pale spots on the basal plate are skeletal spines showing through the coenosarc; a crescent of exposed basal plate is visible round the N.E. side of the colony, where the coenosarc has slightly withdrawn. The colony was about 6 weeks 6 days old, the planula having been extruded on or about 15.xii.28. × 22.



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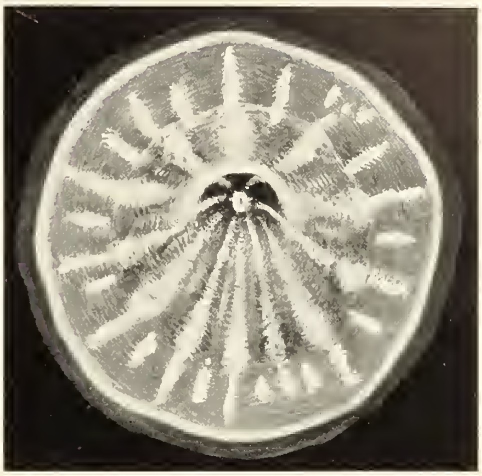

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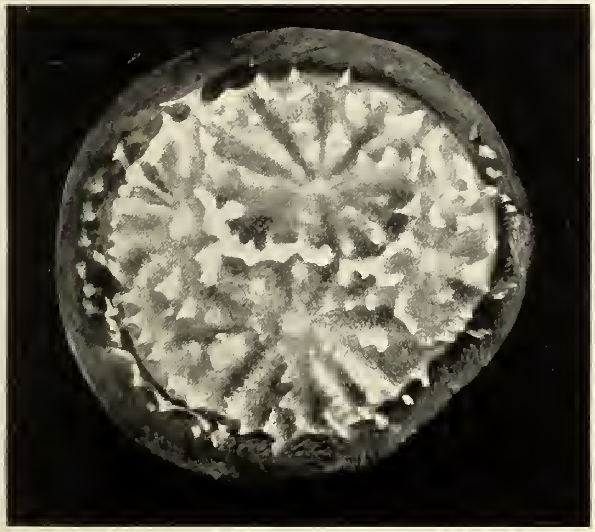

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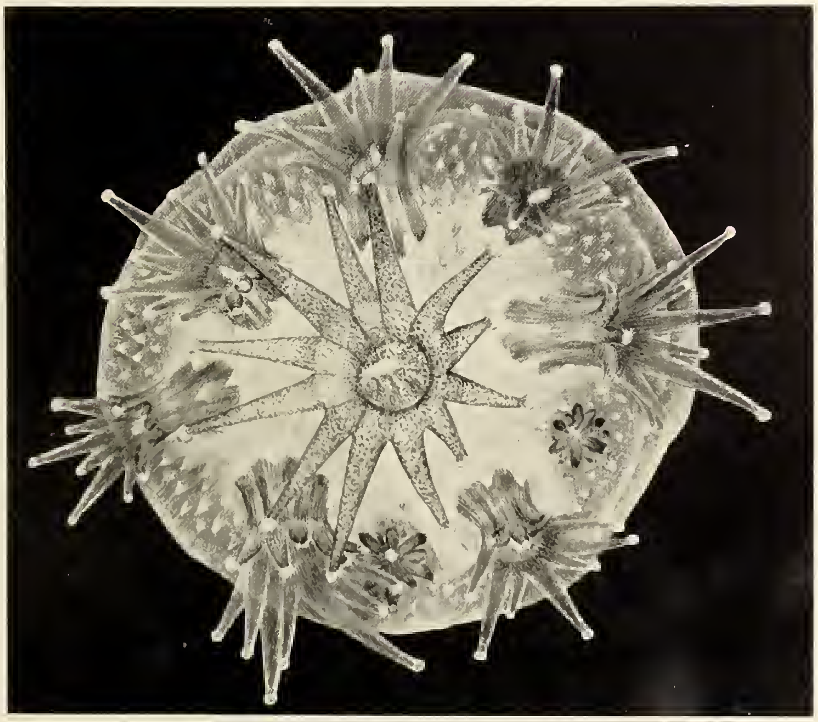

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DESCRIPTION OF PLATE II.

Pocillopora bulbosa.

Fig. 1.—Skeleton of a primary polyp about 6 weeks 5 days old (born on or about 14.xii.28), which still has the septa in a distinct condition, not yet fused into a ring. There are 24 septa in 3 cycles—6.6.12. The basal plate here is much broken. × 12.

Fig. 2.—Stage intermediate between those illustrated by figs. 1 and 3. Same age as those shown in figs. 1 and 3. × 12.

Fig. 3.—A typical corallum at the stage where the septa have fused to form a ring or calyx. Same age as the coralla illustrated in figs. 1 and 2. × 12.

Fig. 4.—Drawing of a stage comparable to that shown in fig. 3, but showing the detail of the spines and of the margin of the calyx. Age of specimen, about 16 days, born on or about 15.xii.28. × 26.

Fig. 5.—Fusion of the corallites of two primary polyps at about the stage represented in fig. 2; and of the same age as the one there figured. × 12.

Fig. 6.—A group of 8 fused corallites, derived from 8 fused polyps. This figure represents part of fig. 7 still further enlarged, and shows more detail. It shows how individual corallites in one and the same colony may be in different stages of formation at the same time, although the planulae giving rise to them were extruded approximately simultaneously. × 7·5.

Fig. 7.—A typical group of corallites, in the positions which their polyps assumed naturally in a finger-bowl. Some of the corallites are not yet included in the general fusion, but had the group lived longer they would all have united into a single colony. The polyps were killed about 16 days after the extrusion of the planulae (which occurred on or about 15.xii.28). × 4·5.

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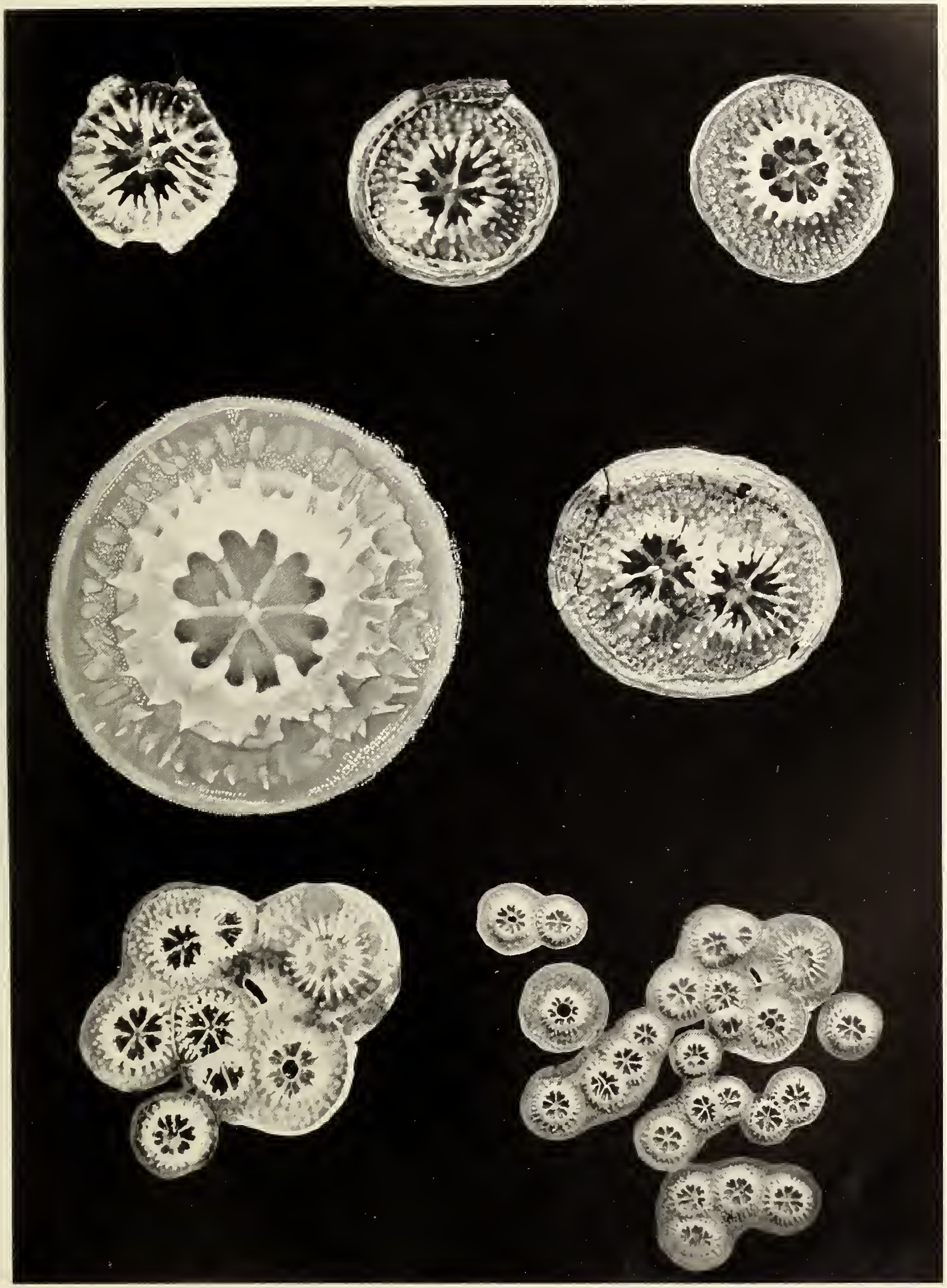

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Photo F. Pittock.
Fig. 4 drawn by Eleanor Dale.

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DESCRIPTION OF PLATE III.

Pocillopora bulbosa.

Fig. 1.—Skeleton of the colony illustrated in Text-figs. 4 and 5, 10 weeks and 6 days after the extrusion of the planula (14.xii.28) from which it was derived. The corallites in the centre have become well thickened; those at the periphery are still composed of relatively slight skeletal elements. × 9.

Fig. 2.—Skeleton of a colony formed from a wild planula which settled in a glass jar placed in about 5 fathoms of water near the mouth of the anchorage. The planula settled between 2.iv.29 and 28.vi.29, and the colony is therefore less than 12 weeks 3 days old, from the time of settlement. It illustrates the relatively stout form which wild colonies tend to assume, in contrast to the thinner disc-like condition more usually assumed by those reared on glass. × 27.

Fig. 3.—Two colonies, each consisting of a primary corallite surrounded by a circle of smaller corallites formed by buds (six in one case, five in the other). This represents the first stage in colony-formation, in its typical condition. The upper colony has a small worm-tube on it. Age of colonies, 7 weeks 4 days; extrusion of planulae, 13.ii.29. × 9.

Fig. 4.—A young wild colony derived from a planula which settled on a drain-pipe planted out in the Madrepore moat. The planula settled between 2.viii.28 and 28.v.29, and the colony is therefore less than 42 weeks 5 days old from date of settling. This figure illustrates the stage at which a sheet of corallites with well-thickened calices has been formed, but no upgrowth to form branches has yet taken place. The colony appears to have been formed by budding from a single primary polyp. The first bud of an incipient branch (S.E. of the primary polyp, and out of focus) has been formed. × 9.

Fig. 5.—A typical reared colony formed by one primary polyp and six primary buds. Note the slight ridge of irregular shape which surrounds the skeletons of the buds, a little way in from the margin of the basal plate (*cf.* fig. 6). Age of colony, 5 weeks 4 days; planula extruded 13.ii.29. × 12.

Fig. 6.—Skeleton of a reared colony with two primary polyps and 9 primary buds in two semicircles. Note the saucer-like ridge surrounding the white central part of the colony. The part outside the ridge had been killed by sediment and algae; the part inside the ridge was alive and healthy; and the ridge is interpreted as a reaction of the coral to sediment and algae (see p. 132). The ridge in fig. 5 is a slighter example of the same condition. Two worm-tubes have been formed on the dead part of the colony. Age of colony, 9 weeks 6 days; planulae extruded 13.ii.29. × 12.

Fig. 7.—Skeleton of a reared colony consisting of two primary polyps and 11 primary buds. In this case the whole outer parts of the colony had been killed by sediment and algae, and only two central areas (whiter than the rest and surrounded by delicate skeletal rings) were still alive. Three worm-tubes have been formed on the dead part, and attached to one end of the colony is the colony of a polyzoan, bearing another worm-tube. Age of colony 9 weeks 6 days; planulae extruded 13.ii.29. × 9.

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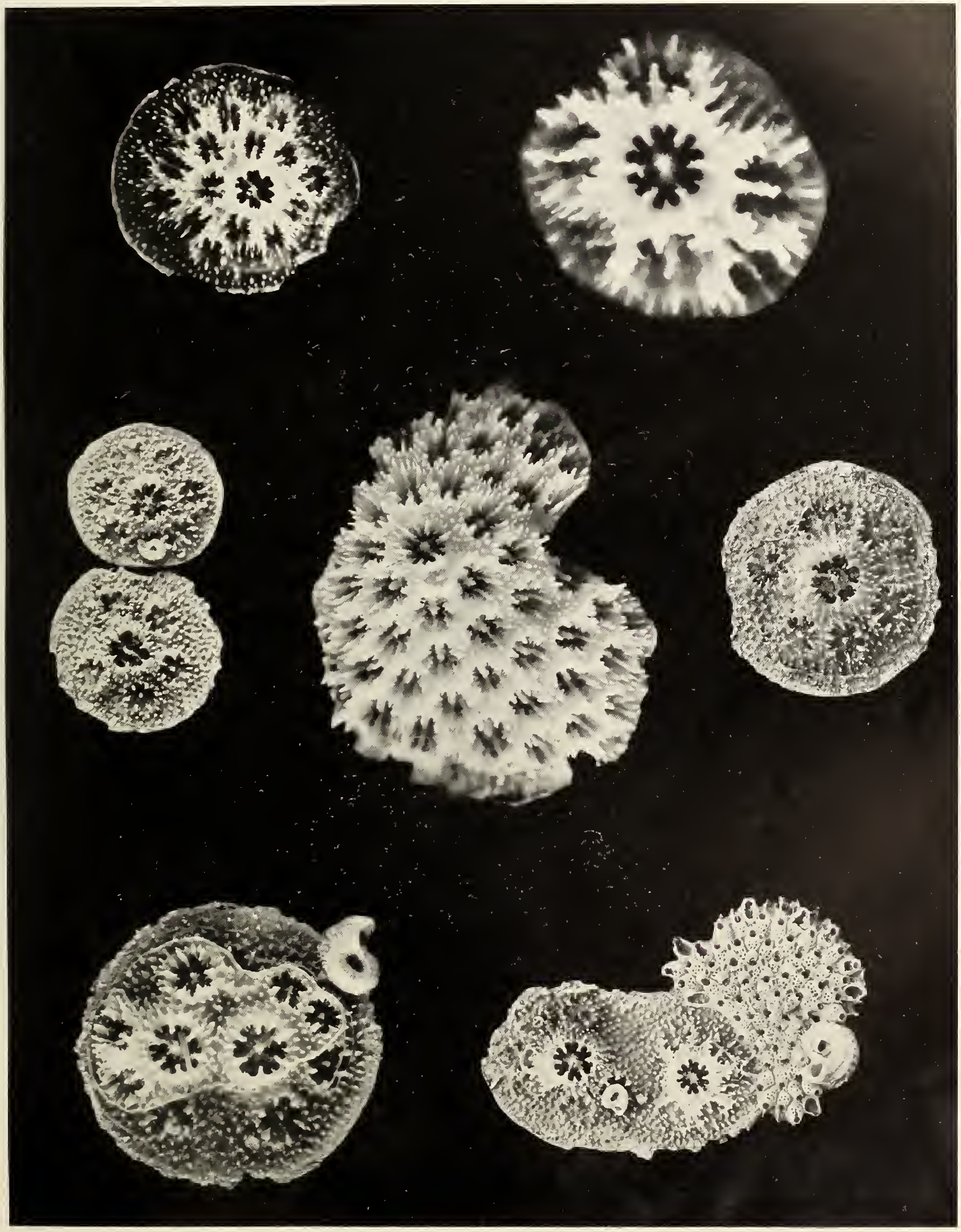

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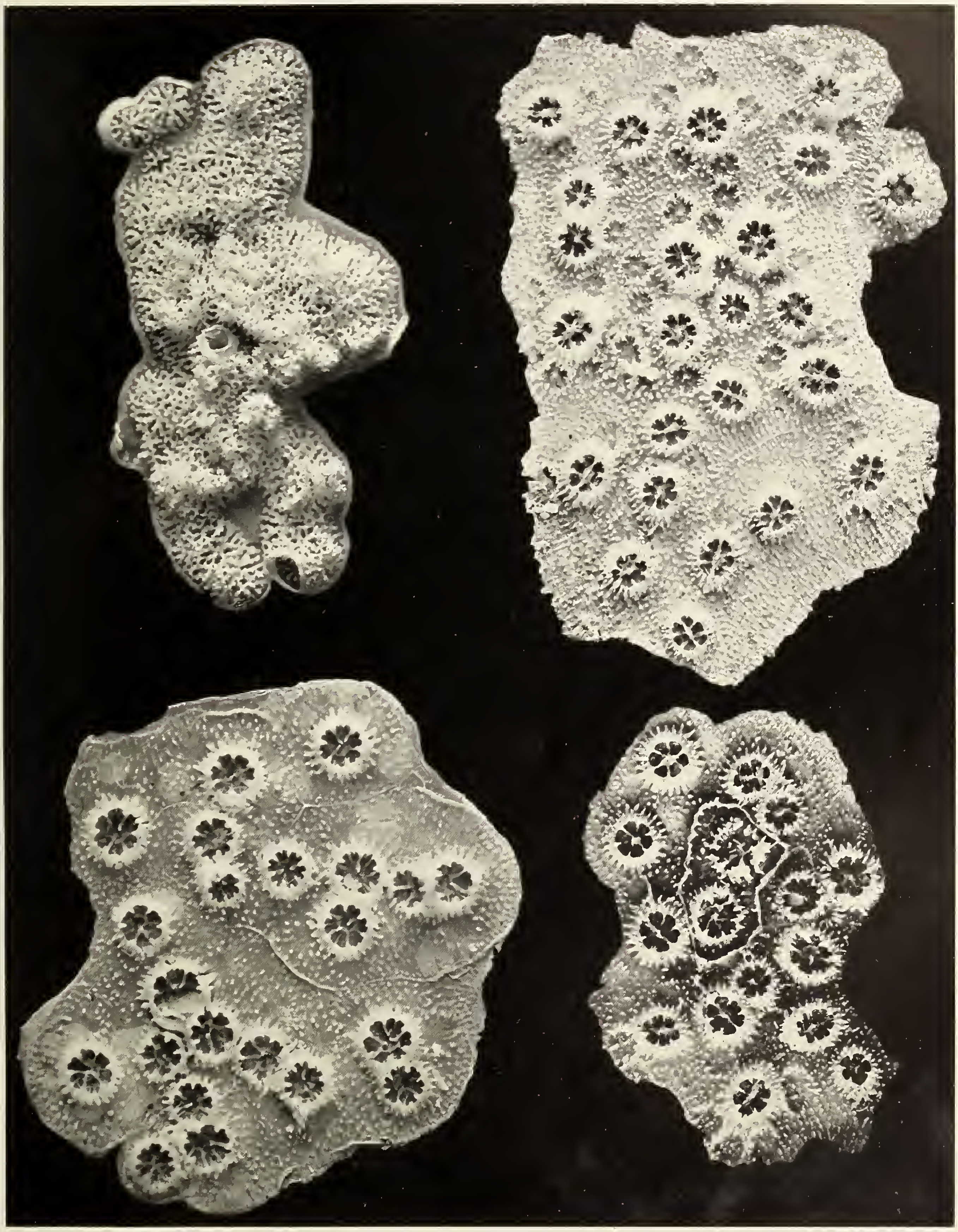
DESCRIPTION OF PLATE IV.

Fig. 1.—Skeleton of a reared colony of *Porites haddoni*, formed by the fusion of a large number of primary polyps. In the upper left-hand corner two corallites have maintained their individuality ; otherwise the corallites form an inextricable mass, among which individuals can be distinguished only approximately or not at all. Variation in the condition of the edge of the basal plate is well shown here—in some places it is flat, in others upturned, elsewhere masked by a strongly-developed inturned edge or parapet. Age of colony 3 weeks 3 days ; planulae extruded 5.ii.29. × 9.

Fig. 2.—Portion of the skeleton of a large reared fusion-colony of *Pocillopora bulbosa* ; it includes 25 primary corallites, and shows the relation to these of the skeletons of a number of buds. It shows also the thorny condition of the basal plate. Age of colony 5 weeks 4 days ; planulae extruded 13.ii.29. × 9.

Fig. 3.—Skeleton of a reared fusion-colony of *Pocillopora bulbosa*, in a less advanced condition than that shown in fig. 2. The corallites of the primary polyps are less fully developed, and budding has only just started. The positions of some buds can be seen as clear places on the basal plate, free from spines. Age of colony about 5 weeks 5 days ; planulae extruded on or about 15.xii.28. (Note that this colony is of the same age as that illustrated in fig. 2, but has developed less far in the time ; probably because it was not put out in the sea at once after its formation.) × 10.

Fig. 4.—Another portion of the colony illustrated in fig. 2, showing a wall-like ring of coral surrounding two primary corallites, and probably induced by a local accumulation of algae and sediment. × 9.



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DESCRIPTION OF PLATE V.

FIGS. 1–3 and 5–9.—Skeletons of young reared specimens of *Porites haddoni*. Those represented in figs. 1, 3, 7 and 9 were 4 weeks 5 days old when killed, and derived from planulae extruded 27.i.29 ; those in figs. 2, 5, 6 and 8 were 3 weeks 3 days old, from larvae extruded 5.ii.29. Fig. 1 shows a skeleton with only a slight development of marginal rim ; fig. 2 a small one with a very strongly developed inturned rim ; fig. 3 an intermediate. Fig. 5 shows a fusion between 2 primary corallites, with a strong marginal wall surrounding both ; fig. 6 a similar case involving 3 corallites. Fig. 7 represents another 3-corallite colony, but here there are skeletal flanges between the corallites. Fig. 8 shows a fusion of 3 with very little marginal wall and no intrinsic flanges ; fig. 9 a fusion of 4 corallites with well-developed flanges between them. Figs. 1, 2, and 5–9, × 9. Fig. 3, × 12.

FIG. 4.—Skeleton of young *Pocillopora bulbosa* which had settled on materials planted out in the Madrepore moat. The materials were put out on 2.viii.28, the coral collected on 28.v.29 ; its age therefore cannot be more than 42 weeks 5 days, and is probably much less. × 9.

FIG. 10.—*Pocillopora bulbosa*. Drawing of the colony represented photographically in Plate III, fig. 2, showing further detail. Note the long columellae of the corallites formed by the 4 primary buds. × 51.

FIG. 11.—A group of young skeletons of *Porites haddoni*, in the natural positions taken up by the planulae in a finger-bowl. The largest colony was formed by fusion of a number of primary polyps, and has developed a system of twisted skeletal flanges. Skeletons 3 weeks 3 days old ; planulae extruded 5.ii.29. × 6·5.

FIG. 12.—Colony of *Porites* from a larva (or larvae) which settled on clean materials fixed in a box in Porites pond. The box was put out 3.viii.28, and the coral collected 29.v.29 ; the age of the colony must therefore be less than 42 weeks 5 days. × 9.

FIG. 13.—Planulae of *Pocillopora bulbosa*, fixed in Bouin and preserved in alcohol. × 12.

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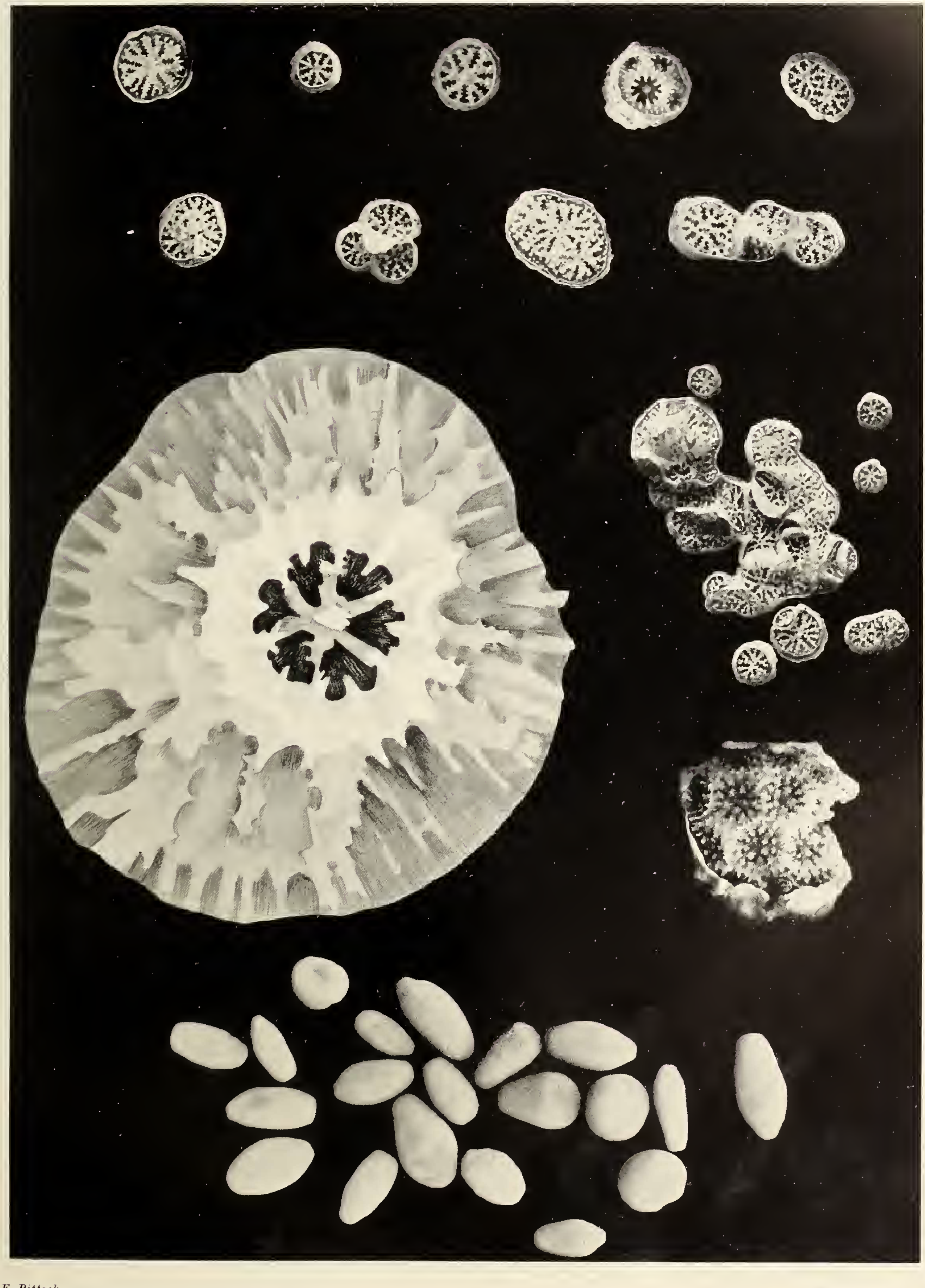

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11

12

13

hoto F. Pittock.
g. 10 drawn by Eleanor Dale.

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DESCRIPTION OF PLATE VI.

Pocillopora bulbosa.

The skeletons represented in figs. 1, 2 and 3 were laid down by colonies derived from planulae which settled on logs fixed in the Madrepore moat. These logs were placed in the sea 2 and 4.viii.28, and the colonies collected 28.v.29 ; their maximum age is therefore 42 weeks 5 days. The skeletons illustrated in the remaining figures are from a series of collected colonies to illustrate growth-stages ; their age is not known. Fig. 9 shows a small adult colony ; the remaining figures show stages of growth down to fig. 1, in which a mound has arisen on the sheet of young corallites, and is about to form the first branch Figs. 1–3 show the development and subdivision of a single branch ; figs. 4 and 5 the independent formation of more than one branch by the basal expansion ; and figs. 6–8 stages between the initiation of branching and the adult condition. Figs. 1–5 illustrate to some extent the difference in form between the calices on the basal expansion and those (*a*) on the stalk and (*b*) towards the apex of branches.

Scale of figures.

Figs. 1 and 2, × 5 diams. ; figs. 3–5, × 4 diams. ; figs. 6–8, × 2 diams. ; fig. 9 is reduced, the actual coral measuring 17·5 cm. in diameter.

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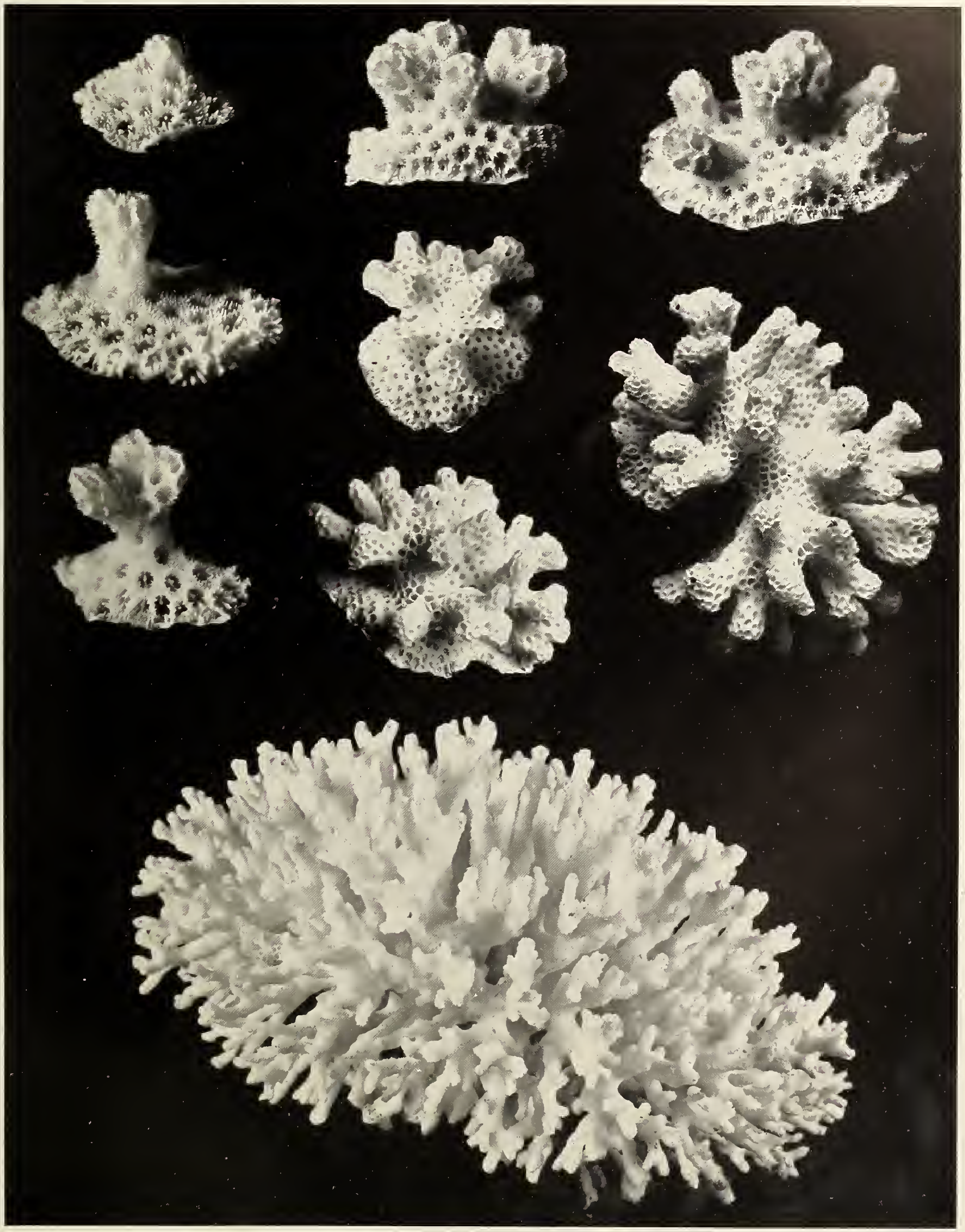

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